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ON SEX-CHROMOSOMES IN HERMAPHRODITISM

RESEARCHES by Boveri and his pupils have shown in certain nematodes, as in arthropods, the existence of two sorts of spermatozoa, one of which contains one more chromosome or chromosome

component than does the other. Eggs fertilized by the one sort of sperm develop into females, those fertilized by the other sort develop into males, as is shown by a cytological study of the two sexes, the female invariably containing the greater number of chromosomes or chromosome components.

Some results of especial interest have been obtained by Boveri[1] from studies of a little nematode (*Rhabditis nigrovenosa*) which occurs as a parasite in the lung of the frog. A free-living generation alternates with the parasitic one. It has long been known that the parasitic generation consists exclusively of females, but the free-living one of both sexes. According to Leuckart and Boveri, parthenogenesis may occur in the parasitic generation, though it is not the exclusive method of reproduction in this generation. For Anton Schneider, recently confirmed by Boveri, found spermatozoa in the genital tract of the parasitic female, and further established the remarkable fact that these spermatozoa develop in the ovarian tubules of the young female herself, which therefore, though a female in external form, is really a hermaphrodite. The close-fertilized eggs of the parasitic worm develop into embryos which are voided with the feces of the host and form the free-living generation, consisting of sexually separate males and females. These produce in turn, from fertilized eggs, the parasitic generation composed exclusively of hermaphroditic females.

The question which Boveri studied was this—how is sex determined in the parasitic generation? Are the spermatozoa of the self-fertilized mother dimorphic, and if so how do they arise?

First of all he established the fact that the spermatozoa found in the parasitic females are of two sorts. The chromosomes may be counted even in the mature sperm, and were found to be in part of the spermatozoa *six* in number, in part of them *five*. In the egg and polar cells were found always six elements. The fertilized egg therefore must contain either *twelve* or *eleven* chromosomes. From one of the former sort doubtless develops a female, from the latter a male. For in the male of the free-living generation Boveri found 11 chromosomes disposed as follows in the spermatocyte of the first order: 5 tetrads, 1 dyad (x chromosome), an arrangement explained as due to splitting of each of the 11 elements, ten of which were disposed in five pairs, forming

[1] "Ueber das verhalten der Geschlechtschromosomen bei hermaphroditismus," *Verh. d. phys.-med. Gesellschaft zu Würzburg*, N. F., 41, pp. 83–97, 1911.

in their split condition tetrad groups, the eleventh being the unpaired x element, as split a dyad. The x chromosome (dyad) passes entire into one of the spermatocytes of the second order, the end result being the formation of spermatids of two sorts, those which contain six and those which contain five chromosomes.

Now arises the first difficulty. If the male individual forms two sorts of spermatozoa, why are not offspring of *both sexes* produced by the free-living generation, instead of females alone? Boveri finds no evidence of degeneration in the spermatozoa containing only 5 chromosomes, and he finds that both sorts are received by the female at copulation, but assumes that the 5-chromosome sort is for some reason incapable of fertilizing the eggs, because from these develop only females containing 12 chromosomes. He relies here upon an analogy with the case of aphids and phylloxerans worked out by Morgan and von Baehr. In those cases, namely, the spermatids with the smaller number of chromosomes fail to develop. In the present case, though developed, they fail, in Boveri's opinion, to function in the fertilization of the egg.

Now comes the second difficulty. If the cells of the (hermaphroditic) female contain *twelve* chromosomes, how does she form spermatozoa containing *five* chromosomes, which is less than the *half-number?* Boveri finds that it is by a peculiar method of cell-division in spermatogenesis. In oogenesis there appear in the oocyte of the first order 6 tetrads which are distributed equally at the maturation divisions. The egg accordingly always contains 6 elements. But in spermatogenesis, in the same hermaphrodite generation, there form 5 tetrads and in place of the sixth a pair of separate dyads which are identified as x-elements. These lag behind the tetrads in division, so that when the five other elements have been distributed in cell-division these two remain at the equator of the spindle. Boveri was unable to ascertain just what does become of them but he assumes that one spermatid lacks them altogether, and this becomes the *male-determining* sperm. What Boveri failed to observe seems to have been observed by W. Schleip,[2] who finds that one x-element passes into half the spermatids, but the other remains on the spindle and does not enter a spermatid. Hence only half the spermatids contain six elements, the others contain five.

Why one process of reduction occurs in spermatogenesis and

[2] *Ber. d. Naturf. Gesell.*, Freiburg i. Br., 19, 1911.

another in oogenesis is unknown. Boveri makes several suggestions without adopting any of them as (1) position of the cells in the egg-tube, (2) seasonal conditions (sperm-production occurs first, egg-production later), (3) unequal plasmatic cell-divisions in the young worm, differentiating sperm-producing from egg-producing tissue.

As regards hermaphroditic animals in general, Boveri maintains that these, when they have the secondary characters of one sex only have that of the female rather than of the male, citing as examples gastropods and cirripeds. Females may retain the capacity to develop sperm, but males do not retain the capacity to develop eggs. For the male state is due to retrogressive variation, loss of cell-constituents, as for example of an x-chromosome. Now in the female this loss may occur *in certain reproductive cells only*, which then become reproductive cells of the male, *i. e.*, spermatozoa. But in the male individual, since *all* its cells are in the reduced state, reproductive bodies characteristic of the female (eggs) can not be produced. Nevertheless the male, though unable to form eggs (which we may assume can come only from a 2x cell) is able to form female-producing *gametes*, those with the full half number of chromosomes.

In its bearing on general theories of sex-determination Boveri's paper is important. It provides a way of reconciling the opposed views that sex-determination is independent of environmental influences and that it is dependent upon them. Both views are correct in part.

Sex is apparently in all cases controlled by cell structure, a clear index of which is afforded by the number of the chromosomes found in the nucleus. The more complete, or fully duplex, state is in all cases characteristic of the female; a more reduced state, either partially duplex or simplex, is characteristic of the male. But *external conditions* may influence the cell-constitution, and so indirectly determine sex. This is known to be the case in parthenogenesis and according to Boveri's observation in this paper it may be true in hermaphroditism also. Thus in rotifiers and daphnids abundant nutrition causes the unfertilized egg to develop without undergoing reduction, *i. e.*, in the fully duplex (2N) condition, and a female results; poor nutrition causes the unfertilized egg to delay development until maturation is complete and it has passed into the simplex condition, and a male results. The protoplasmic differences in the two cases are not confined to differences in chromosome number, the cell

size is also different, the female egg being larger. But the size-difference is not all-important, either, for the winter egg of the rotifers or daphnids is still larger, yet undergoes complete reduction, but will not develop in this condition unless fertilized; then it produces a female, being in the fully duplex, 2N condition. Sex in such cases is correlated with a particular cell-constitution, but this cell-constitution may be influenced by the environment; hence the environment may *indirectly* control sex.

Boveri's present contribution adds another important case to those previously on record. In the nematode, too, protoplasmic conditions control sex, but it is quite possible that external agencies as yet not identified may in this case also determine those protoplasmic conditions and so indirectly determine sex.

The question naturally arises whether the same may not be true in the higher animals also, those which are sexually separate. This idea has been strongly advocated from time immemorial, and still has its adherents, but a really critical analysis of the evidence shows that it rests on a very insufficient basis. In fact the experimental evidence is almost conclusive against it.

There is no *a priori* reason why the cell structure which differentiates male-producing from female-producing gametes or zygotes should not be controllable through environmental agencies in the higher animals, as in parthenogenetic animals. But *is* it? This is a question of fact, in determining which we must weigh evidence. The really critical examination of such evidence was begun in 1900 by Cuénot in a notable paper published in in the *Bulletin Scientifique,* and has been followed up by several others who have carried out carefully planned experimental researches, as, for example, Oscar Schultze. Their evidence is almost wholly against the idea that sex in the higher animals can be controlled either directly or indirectly. Russo,[3] indeed, still maintains this view. He holds that by feeding or injections of lecithin the structure of the ovule in the rabbit ovary may be altered, and that a female embryo develops from such altered ovules. Now there are two questions of fact involved in this evidence, first whether the cell-structure described by Russo is induced by the lecithin treatment or by some other agency. This is a question for cytologists to answer. The second question is whether the cell structure described has anything to do with sex-determination. This is a question in part for the experimental breeder to answer. From this point of view I have elsewhere

[3] *Biol. Centrbl.,* 1911.

discussed Russo's data. Two independent repetitions of his breeding experiments, one made in Italy, the other in England, have failed to confirm his conclusions, which therefore, as matters stand, have slight weight.

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NOTES ON ICHTHYOLOGY

IN the *Abhandlungen of the Akademie der Wissenschaften*, in Bavaria, Vol. IV, Münich, 1910, Victor Franz has an elaborate account of the bony fishes collected in Japan by Haberer and Döflein. This is an important paper, containing descriptions and figures of numerous new species.

In the Contributions from the Zoological Laboratory of Indiana University, No. 76, part 2, Dr. Carl H. Eigenmann gives a "Catalogue and Bibliography of the Fresh-water Fishes found in Tropical and South Temperate America," including all south of the latitude of the mouth of the Rio Grande. Dr. Eigenmann gives a discussion of the valid reasons which have led him to retain the generic name *Æquidens* in place of *Acara*.

In the *Bulletin of the Bureau of Fisheries*, Vol. XXIX, 1909, Jordan and Evermann discuss the "Salmonoid Fishes of the Great Lakes," with numerous plates, some of them in color. The name *Leucichthys* of Dybowski is adopted in place of the earlier name, *Argyrosomus*, of Agassiz, which was first used for a marine fish. Four new species of *Leucichthys* or lake herring are described, *L. supernas* from Lake Superior, *L. cyanopterus* from Lake Superior, *L. manitoulinus* from Lake Huron, and *L. ontariensis* from Lake Ontario. A new variety, *L. harengus arcturus,* is described from the west end of Lake Superior. Two new sub-generic names are adopted: *Thrissomimus* Gill for the ordinary lake herring, the name *Argyrosomus* being preoccupied; and *Cisco* for the deep-water forms. In this paper it is shown that the shore lake herring, instead of constituting a single species, are really several in number, at least six of them in the Great Lakes deserving recognition as species.

In the *Bulletin of the Bureau of Fisheries,* Vol. XXIX, 1909, Dr. Charles W. Greene discusses in detail the migration of the salmon in the Columbia River, treating with considerable fullness the methods by which individuals may be marked.